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Das Basipodium von Anthracobunodon weigelti *HELLER, 1934 (Artiodactyla, Mammalia) aus dem mittleren Eozän des Geiseltales bei Halle (Deutschland)*

With 2 figures, 5 tables and 2 plates

JÖRG ERFURT & JÖRG HABERSETZER

Abstract: The carpus and tarsus are described of the middle Eocene haplobunodontid *Anthracobunodon weigelti* from the lignite beds of the Geiseltal (MP 13). The study is based on new methods of microradiography and computer-tomography which allow a classic and a three-dimensional investigation of morphological details. The reconstructed morphology of the basipodium is compared with other artiodactyls of the Eocene and interpreted phylogenetically. *Anthracobunodon* displays a paraxonic foot with typical artiodactyl astragalus and calcaneum. Navicular and cuboid are unfused. An entocuneiform and an ectocuneiform exist distally, which are probably fused with the mesocuneiform. The carpus displays the beginning of the paraxonic arrangement still without any fusion. The carpals are in two rows with four bones each. Five metacarpals are retained, the first of which is reduced to half the length of the others, the third is the longest. In the foot the main metatarsals have about the same length, the first metatarsus is reduced. Both extremities are characterised by hooflike third digits.

Zusammenfassung: Es werden die Hand- und Fußknochen des mitteleozänen Haplobunodontiden *Anthracobunodon weigelti* aus den Braunkohlenschichten des Geiseltales beschrieben (MP 13). Die Studie basiert auf neuen Methoden der Mikroradiographie und Computertomographie, die sowohl eine klassische als auch eine dreidimensionale Untersuchung morphologischer Details erlauben. Die rekonstruierte Morphologie des Basipodiums wird mit anderen Artiodactylen des Eozäns verglichen und phylogenetisch interpretiert. *Anthracobunodon* zeigt einen paraxonischen Fuß mit den für Artiodactylen typischen Astragalus und Calcaneus. Naviculare und Cuboid sind nicht verwachsen. Distal existiert ein Endocuneiforme und ein Ectocuneiforme, das vermutlich mit dem Mesocuneiforme verwachsen ist. In der Handwurzel zeichnet sich der Beginn einer paraxonische Anordnung ab, die noch keine Verschmelzungen erkennen läßt. Der Carpus besteht aus zwei Reihen mit jeweils 4 Knochen. Es sind noch fünf Metacarpalia erhalten, wobei das erste auf die halbe Länge der anderen reduziert ist. Längstes Metacarpale ist das dritte. Am Fuß sind drittes und viertes Metatarsale fast gleich lang, das erste ist reduziert. Beide Extremitäten sind durch Hufe als Endphalangen charakterisiert.

1 Introduction

The syndrome of specially formed tarsal and carpal bones in connection with the paraxonic arrangement of the metapodials is crucial for the evolution of early artiodactyls. The astragalus is significant, characterised by proximal and distal trochlea that are more or less uniform for all fossil and living artiodactyls. Several papers give morphological descriptions of this bone and point out possible ways of evolution. The first modern descriptions of the tarsus were given by GUTHRIE (1968) for the Lostcabinian *Bunophorus* and *Diacodexis,* followed by papers of ROSE (1982, 1985). The early Eocene *Diacodexis pakistanensis* was described as the most primitive postcranial artiodactyl remains by THEWISSEN & HUSSAIN (1990). The complete composition of the carpal and tarsal skeleton of Eocene artiodactyls is, however, still relatively unknown.

In the middle Eocene lignite beds of the Geiseltal near Halle (Saxon-Anhalt, Germany), skeletons of artiodactyls are well preserved, including diacodexeids, dichobunids, cebochoerids and haplobunodontids (ERFURT & HAUBOLD 1989). This material is investigated here on the basis of improved X-ray methods in order to obtain, in a non-destructive way, more information concerning the construction of the basipodium of *Anthracobunodon weigelti*. These methods were applied to the Geiseltal material for the first time in order to avoid additional preparations of the fragile fossils. The result of this study is one aspect of a current three-dimensional body reconstruction of this haplobunodontid.

2 Materials and methods

Most of the artiodactyl skeletons from the Geiseltal valley were excavated before 1945. At the time paraffin was used to embed bones in a frame of plaster. Applying this technique, the bones are impregnated by paraffin resulting in a rather poor consistency. The exchange of paraffin with other stabilisers is still an unsolved problem of preparation.

Microradiographic X-ray methods of HABERSETZER (1991, 1994, 1995) provide a new approach for investigation of the Geiseltal material. Specimens were studied with two different specially adapted non-destructive (NDT) X-ray procedures. We used a Hewlett Packard Faxitron 43855 industrial X-ray-tube with a focal spot size of 0.5mm. Specimen were placed on a horizontal film plate 90 cm from the focal spot. Close contact of the fossil with the film maximises sharpness needed for later magnification. All images were obtained with a double coated non-destructive testing X-ray film (AGFA D7) processed 4 times longer compared to medical X-rays. Radiological results were enhanced by the application of high speed scanning and digital imaging of NDT X-ray plates using a computer. In this study we used predominantly the newly described ***C***omputer ***A***ided ***C***ontact ***M***icroradiography (***CACM***, SULLIVAN et al. in press) which provides high contrast and grainfree images with magnification of morphological details of up to 8x (with AGFA D7) which cannot be achieved with normal medical X-ray films. Magnifications of microradiographs were obtained using a 12bit Camera Scanner and a 35mm ZEISS C-mount Macro Lens (Kontron Progress 3012). This scanner was used with a specially modified software for NDT films with high densities which allows binning of 4 pixels to a low noise output pixel. Spectral fitting of the Camera Scanner to a powerful scanning light (Radx brite light) additionally resulted in a increased grey scale of the digitised microradiographs. After transfer of 12bit/8bit images to a PC workstation digital imaging was accomplished prior to producing the final print.

In order to freely tilt and rotate specimens in the X-ray beam to obtain various angles of views, we also used another newly described digital radiological procedure: ***C***ontinuous ***O***nline ***R***ecalibrated ***R***adiography (=***CORR***, MORLO & HABERSETZER, in press). The X-ray source was a microfocus tube (Feinfocus FXE-150) with a spot size of 5µ by 7µ allowing a large distance between the specimen and the X-ray image plane. The specimen holder was the fourth version of a manipulator with isocentric tilt and rotation capabilities. The X-ray sensitive medium was an image intensifier with attached video-camera (Hitachi KP-M1) and a real time 16-bit-video processor (HAMAMATSU DVS 3000) with a 8-bit imaging computer interface. The main advantage of this setup compared to industrial composed equipments is the combination of DIMA (direct magnification radiography) with a real-time 12-bit-video processing of excellent analogue gain/contrast preamplification and jitter-free synchronisation to the analog/digital converter. This extreme dynamic range allows a continuous online recalibration of 8-bit grey scale images within a 16-bit window for each particular detail of the fossil before the image is frozen and stored on a PC for (only minor) further processing.

Conventional computer-tomography (CT) was applied in addition to the investigations mentioned above with a "Somatom Plus S" by SIEMENS in the Röntgenklinik of the Martin Luther University Halle. The carpus and tarsus of Ce III-4221 were scanned transversally from cranial to caudal side. The thickness of the slices was about 1mm.

In the anatomical descriptions of the material the following acronyms are used:

AMNH - American Museum of Natural History, New York;
NMB - Naturhistorisches Museum, Basel;
GMH - Geiseltalmuseum, Halle;
HGSP - Howard University Geological Survey Pakistan;
MNHN - Muséum National d'Histoire Naturelle, Paris;
PIN - Paleontological Institute Russian Academy of Sciences, Moscow;
SMF - Senckenberg Museum, Frankfurt;
UM - Université de Montpellier, Laboratoire de Paléontologie des Vertébrés E.P.H.E., Montpellier;
USGS - United States Geological Survey, Denver.

The letters and roman numbers after GMH describe the pit within the Geiseltal valley. The number indicates the individual fossil within this pit. For example Ce III-4221 stands for specimen number 4221 of the pit "Cecilie III" in the Geiseltal valley (HAUBOLD & THOMAE 1990). The study was carried out mainly based on the following determined articulated skeletons, all belonging to the collection of the Geiseltalmuseum Halle:

Anthracobunodon weigelti: GMH Ce II-4225 lectotype; Ce II-4226 paralectotype, HELLER (1934: pl. 21); Ce II-4219; Ce III-4221; Ce IV-4223; Ce IV-4332; Ce IV-4334;
Haplobunodon mülleri: GMH XXII-553;
Gervachoerus jaegeri: GMH Ce III-4220;
Masillabune franzeni: GMH VII-58.

The most complete specimen is GMH Ce III-4221 (see Plate 1A) with skull, thorax, tail, both forelimbs and parts of the right hindlimb. In addition to the skeletons mentioned above other postcranial material (mostly isolated tarsals) is also used for comparisons. So far as possible determinations were made by correlation of size to tooth features with other specimens with dentition.

3 Anatomical description of carpus and tarsus

3.1 Carpus

Specimen Ce III-4221 displays both forelimbs with both articulated carpal skeletons. The left side is medially visible, the right side laterally (see Plate 1A). Both hands have a strong inflection between zeugopodium and metacarpals. The proximal row is articulated with radius and ulna, the distal row is connected with the five metacarpals. The inflection of the hand is due to a dislocation inside the carpal bones. In addition, elements of the proximal row are dislocated into the distal carpal bones on the right extremity. Unfortunately, no isolated carpals were found in other Geiseltal material. Therefore, most measurements were taken from microradiographs or computer-tomographs.

Tab. 1: Carpal measurements of *Anthracobunodon weigelti* GMH Ce III-4221 from the Geiseltal [in mm].

A: largest length cranio-caudal B: largest width medio-lateral C: largest height dorso-volar (ventral)

carpal bone	A	B	C	remarks
Os carpi accessorium s	8.5	2.0	3.1	A, C X-ray; B: smallest diameter in the middle of the bone; CT
Os carpi accessorium d	8.9	2.9	3.5	A, C X-ray; B: smallest diameter in the middle of the bone; CT
Os carpi ulnare s	-	2.9	5.2	B,C: CT see Plate 2E/8
Os carpi ulnare d	6.2	3.2	5.2	B: CT
Os carpi intermedium s	6.0	6.3	6.0	A: X-ray
Os carpi intermedium d	-	-	6.0	
Os carpi radiale s	7.3	4.6	5.4	B: CT see Plate 2E/7
Os carpi radiale d	7.5	4.9	-	
Os carpi quartum s	7.6	(5.3)	5.1	A, B: CT see Plate 2E/7; B width in the middle of the bone
Os carpi quartum d	(6.7)	6.3	5.0	A: CT, B width in the middle of the bone
Os carpi tertium s	3.8	4.6	4.5	A: X-ray
Os carpi tertium d	-	4.3	(3.5)	B: CT
Os carpi secundum s	3.7	2.6	-	A-C: X-ray; A, B: CT see Plate 2E/9
Os carpi secundum d	-	2.5	4.0	B, C: CT
Os carpi primum s	2.4	1.0	2.0	A,C: CACM; B CT see Plate 2E/10
Os carpi primum d	-	1.0	1.8	B,C: CT

3.1.1 Os carpi accessorium (Pisidium)

The longish accessorium is in contrast to all other carpals. The bone is about 8.5mm long and slightly crooked. In GMH Ce III-4221 it is visible directly in contact with the distal end of the ulna. Both ends are thick, giving the bone the shape of a dumbbell. The lateral end is convex and characterised by a tuberositas for the musculus flexor carpi ulnaris. In lateral X-ray view it is oval and about 3.5mm long and 1.0mm high. The CT gives a width of 3.0mm and shows a high spongiosa density comparable to a joint. The proximal end is round and slender with a largest diameter of about 2.7mm. It displays two small articulation surfaces, a dorsal surface for the articulation with the ulna and a volar surface for the ulnare. The accessorium is similar to *Masillabune franzeni* GMH VII-58, visible in lateral position. The dimensions are: length 8.6mm, and width of the proximal end: 3mm. Again, the distal end is thicker and broader at 4.1mm. In comparison to *Caenotherium* sp. NMB Sau.-1499a (HÜRZELER 1936: Plate IV/25,26) the accessorium of this haplobunodontid is slender.

3.1.2 Os carpi ulnare (Cuneiform)

The ulnare is seen laterally on the right extremity. This side is convex and has a rectangular shape. The main part of the dorsal side is used for the articulation surface with the ulna, which is longish and saddle-shaped. Additionally a round and concave facet for the accessorium exists caudolaterally from here. In the CT (see Plate 2E/7,8) the ulnare is - like the radiale - higher than it is wide: 4mm on the dorsal border and 3mm on the volar border. The largest diagonal from the craniodorsal to the caudovolar border is 6mm on the lateral side of the right hand. Medially a convex joint exists for the intermedium. A small prolongation on the dorsal border, which fits with the intermedium, indicates that the ulnare stands a little bit higher than the intermedium. The volar articulation surface is planar to slightly concave for the os carpi quartum.

3.1.3. Os carpi intermedium (Lunar)

The intermedium is directly visible on the left and right extremity. Standard X-ray and CT gives a T-form shape in volar or dorsal view which strongly resembles the Oligocene *Caenotherium* sp. NMB Sau.-1495a (HÜRZELER 1936: Plate IV/18-21). The long axis runs between ulnare and radiale and fixes the bone like a wedge. The length is about 6mm. In the anterior view, see Plate 2G/2, it has a trapezoid shape with a shorter lower border. The medial side runs straight, the lateral side is gently concave. The joint is 5mm broad on the dorsal border, on the volar one 4mm. The articulation surface for the ulnare is concave, giving a slit between these carpals. A similar slit, built by the intermedium and the radiale is to be found in the recent *Sus*. The facet for the radius is more or less planar and for radiale convex. *Anthracobunodon* displays a little tip dividing the volar border into two nearly equal joints. In contrast to *Caenotherium* sp. it is clear that quartum and tertium were not separated by the intermedium. This observation is supported by the lesser height of the intermedium in comparison to the height of the ulnare plus the height of the tertium.

3.1.4 Os carpi radiale (Scaphoideum)

The radiale is the longest carpal in the proximal row (Tab. 1) and forms the largest joint to the forearm. The bone is laterally seen on the right extremity and dorsally on the left. In medial view the bone is rectangular and displays a convex surface which is porous like the other carpals. The dorsal side resembles a semicircle with the straight side face to face to the intermedium. It contains a longish groove and a convex facet in correlation with the divided trochlea radii. The groove lies on the anterior side and is medio-laterally orientated. Younger artiodactyls, such as *Caenotherium* sp. NMB Sau.-1492a (HÜRZELER 1936: Plate IV/13-16) or *Praetragulus* PIN 3110/1207 (VISLOBOKOVA 1998: Fig. 7/e) have a slender radiale with a smaller articulation surface in comparison to the intermedium. *Anthracobunodon* has a radiale of trapezoid shape in transversal section with a mainly planar volar border, see Plate 2E/5-7. On this side two concave joints are embedded. The anterior one serves the connection with the tertium. The smaller posterior one is regarded as joint for a secundum. In anterior view, the facet for the intermedium is convex.

3.1.5 Os carpi quartum (Unciform)

The most massive carpal is the quartum. The right quartum lies in the matrix, but has good visibility in the CT-reconstruction, see Plates 2G and 2H. The left quartum is dislocated underneath the metacarpals, see the CACM in Plate 1B/15. In lateral view the bone reveals a cube-shaped form. The outside is rough. Dorsally it displays a slightly convex facet for the ulnare. Laterally a small facet is visible, probably for the MC V. Unfortunately the head of MC V is not directly visible. Other articulation facets of the quartum are not to be seen. The volar side is concave-arched and directs a relatively long process visible in cross-section Plate 2E/7. This tapering process gives the bone a triangular outline in dorsal (respectively volar) view. The process correlates to a caudal prolongation of MC III and MC IV as well. Due to the large contact area of MC IV and MC V this part of the distal carpals seems especially significant for transmission of the body weight. Medially the quartum articulates with the tertium and dorsomedially with the intermedium. Due to the prolongation of MC III in comparison to MC IV, it may articulate with both main metacarpals, proximally. The process on the head of MC III fits in the outline of the quartum.

3.1.6 Os carpi tertium (Magnum)

The tertium lies exposed on the left hand. Anteriorly viewed it displays a longish pentagonal outline with the tip to the dorsal side. There exist two slightly concave facets, the bigger one for the intermedium, the smaller for the radiale. The lateral and medial margin are straight, giving planar facets for the secundum respectively the quartum. The cross-section in Plate 2E/6 indicates a longish rectangular shape which fits into a concavity of the quartum. A small swelling is visible on the caudal margin, which could indicate the base of a caudal prolongation known from *Caenotherium* sp. NMB Sau.-1502a (HÜRZELER 1936: Plate V/7). Unfortunately the section does not cover the complete diameter. Therefore the definite contour is uncertain. It seems that in *Anthracobunodon* the tertium is wider than longer compared with *Praetragulus* (VISLOBOKOVA 1998: Fig. 7). The volar articulation surface is convex, giving a close contact to the caput of MC III.

3.1.7 Os carpi primum (Trapezium) and secundum (Trapezoid)

One part of the secundum is seen on the left hand, compare Plate 2F/5. It follows medially from the tertium. In the transversal section, see Plate 2E/9 the outline is rectangular, higher than wider. For the radiale a concave facet exists dorsally. In correlation with the tertium the lateral articulation surface should

be more or less planar. Dur to the convex head of the MC II the volar facet is supposed to be concave.
The primum stands out in the CACM near the caput of the MC V, see Plate 1B/22. Its shape of a pea resembles that of a sesamoid. With dimensions less than 1mm the lower limit of resolution is reached for the applied computer - tomograph. In the CACM this smallest carpal still displays a planar facet for the articulation with the MC I. In contrast to other middle Eocene artiodactyls this metacarpal is thin, but still relatively long. From lateral to medial side the relation of the lengths between the fifth and the other metacarpals are about 1: 1.25 : 1.36 : 1.1 : 0.7.

3.2 Tarsus

Due to the compact construction astragalus and calcaneum are relatively frequently represented in the Geiseltal collection. GMH Ce III-4221 has a nearly complete right hindlimb, see Plate 1a and 1c. The tarsus is laterally visible. A fracture runs through the distal row, dividing the tuber calcanei from its basal part and destroying smaller tarsals. The astragalus is completely visible, standing in articulation with tibia and navicular. In order to investigate the other components of the tarsus a CORR - analysis was undertaken for specimen GMH Ce IV-4332. The determination as *Anthracobunodon weigelti* is based on the high similarity of calcaneum and astragalus between this specimen and GMH Ce III-4221. Additionally to the articulated skeletons, 30 isolated astragali and 12 isolated calcaneis are also preserved.

3.2.1 Calcaneum

The calcaneum is marked by a basal part and a prolongated tuber calcanei that is a distinguishing feature for all artiodactyls. The relation of basal part to the tuber is about 1:2. In the Geiseltal artiodactyls the lateral side of this tuber has a deep longish groove, running over two thirds of the total length. The groove comes slightly to an end dorsally and is open on the plantar side, creating a trail for the strong ligaments between calcaneum - fibula, calcaneum - cuboid and calcaneum - metatarsus. Furthermore, the groove serves for the fixing of the ligaments between tibia - calcaneum and astragalus - calcaneum. The medial side is smooth and round.

Tab. 2: Calcaneum measurements of Geiseltal (GT) artiodactyls compared with European taxa [in mm].

A: total length of the calcaneum from tuber calcanei to the plantar articulation facet
B: length of tuber calcanei from the dorsal side of the sustentaculum tali to the top of the tuber
C: largest height of proc. coracoideus dorso-plantar
D: largest width of the sustentaculum tali medio-lateral

species	locality	A	B	C	D	remarks
Anthracobunodon weigelti GMH CeII-4219	GT, MP 13	31.0 s	15.1 s	12.3 s	-	laterally visible
A. weigelti GMH Ce VI-2800	GT, MP 13	33.9 d	17.2 d	13.7 d	8.3 d	isolated
A. weigelti GMH Ce IV-4332	GT, MP 13	33.5 s	15.6 s	12.9 s	-	B-D: X-ray
A. weigelti GMH Ce IV-4334	GT, MP 13	30.5 s	15.2 s	12.9 s	-	B-D: X-ray
Anthracobunodon? GMH XXXVII-126	GT, MP 13	(30) s	-	12.3 s	8.6 s	isolated; tuber calcanei broken
Meniscodon picteti GMH XLI-24	GT, MP 13	37.9 s	21.7 s	(16) s	10.0 s	isolated; proc. Coracoideus broken
Haplobunodon? GMH XLI-210	GT, MP 13	32.4 d	16.7 d	12.5 d	(7) s	X-ray; sustentaculum broken
Masillabune franzeni GMH VII-58	GT, MP 13	32.1 d	17.2 s	13.5 s	-	lateral visible
Dichobunidae? GMH Leo I-2807	GT, MP 13	23.4 s	11.6 s	10.3 s	6.5 s	isolated; proc. Coracoideus broken
A. neumarkensis? GMH XVIII-3605	GT, MP 12	(26) s	11.5 s	10.9 s	-	isolated; sustentaculum broken
Haplobunodon mülleri GMH XXII-553	GT, MP 12	30.3 d	14.8 d	-	7.9 d	isolated
Haplobunodontidae? GMH XXII-789	GT, MP 12	30.3 d	15.5 d	-	7.8 d	isolated; proc. Coracoideus broken
Messelobunodon? schaeferi SMF ME-1001	Messel, MP 10	25.9 s	13.8 s	10.1 s	-	lateral visible
Messelobunodon schaeferi SMF ME-501	Messel, MP 10	34.7 d	17.8 s	(14) s	(11) d	C-D: X-ray
Aumelasia gabineaudi SMF ME-1527	Messel, MP 10	31	-	-	-	FRANZEN (1988: Tab.1)
Aumelasia gabineaudi coll. POHL	Messel, MP 10	30.5 d	(14) d	(10) d	-	A-C: measurement from X-ray's
Diacodexis metsiacus USGS 2352	Wyoming, Yale 55	20.2 s	10.9 s	8.0 s	6.1 s	measurement from cast ROSE

In the Geiseltal material the biggest calcaneum of *Anthracobunodon* is that of Ce VI-2800. There, the tuber has an ellipsoid diameter of about 8.2 x 4.8mm and tapers dorso-ventrally. The end of the tuber is swollen rounded with a prolongation in medial direction carrying a thin furrow, sagittal orientated. Above this furrow extends a smooth triangular area, which is clearly visible in the bigger calcanei of *Anthracobunodon*, but poorly marked in the small GMH Leo I-2807, determined as dichobunid.
The proc. coracoideus is well developed in the first third of the total length of the bone. In lateral view it displays a round lobe. The dorsal rim is completely developed as articulation facet for the fibula. The upper margin of the medial side displays a pronounced, planar, half moon-shaped facet for the astragalus. The lower part of the process is rough as is most of the medial side of the basal part. Laterally in

GMH XVIII-3605 the process has an articulation facet on the upper margin, which is absent in GMH XXXVII-126 and GMH Ce IV-2800. This contrast is interpreted as the reduction of the fibular facet in younger haplobunodontids.

The sustentaculum tali straightens up perpendicular on the medial side. It has a wide basis and tapers to the end. Therefore this process is often broken. On the plantar outside it displays a sulcus for the tendon of the musculus flexoris digitalis lateralis. The inside is completely formed as a concave articulation surface for the pillow-shaped sustentacular facet of the astragalus. On the medial corner there exists a second, smaller, planar facet corresponding to the medial wall of the sustentacular facet on the astragalus.

The triangular basal part of the calcaneum occupies one third of the total length. On the lower margin of the medial side is the third, longish-rectangular facet for the astragalus. This facet reaches the distal top of the calcaneum and has dimensions of about 7.5mm x 2.5mm on GMH Ce IV-2800. On the plantar side the calcaneum displays a well-marked concave facet for the cuboid. This convex joint is rectangular with a dimension of about 8.3mm x 4.5mm for the same specimen. It is obliquely orientated medio-laterally and cranio-caudally as well. In correspondence stands the proximal facet on the cuboid. The medio-lateral orientation is interpreted to divert axially the pressure of the body mass. In dorsal (proximal) prolongation of this facet a distinctive, deep notch is found on the caudal edge of each calcanei. The other areas of the medial side are also rough, highlighting the joints. The small dorsal side is rough too with a little triangular dip. In all, the calcaneum extends no longer in plantar direction than does the astragalus, meaning that both tarsals of the proximal row end more or less on the same level viewed laterally.

3.2.2 Astragalus

Due to the taxa represented in the Geiseltal the astragali in Tab. 3 show a relatively large variation in their dimensions and proportions as well. Nevertheless, all consist of a deep tibial trochlea and a medially deflected distal trochlea (caput tali) which is characteristic for all fossil and living artiodactyls.

Tab. 3: Astragalus measurements of Geiseltal (GT) artiodactyls compared with European taxa [in mm].
A: largest length between the proximal and distal trochlea
B: largest width of the distal trochlea medio-lateral (parallel to the lateral and medial border)
C: largest height in the middle of the astragalus dorso-plantar

species	locality	A	B	C	remarks
Anthracobunodon weigelti GMH Ce II-4219	GT, MP 13	16.2 s	8.5 s	6.4 d	X-ray
A. weigelti GMH Ce II-4226	GT, MP 13	16.5 s	8.4 s	8.0 s	isolated
A. weigelti GMH Ce III-4221	GT, MP 13	(14) d	-	6.7 d	X-ray; A: proximal part faulty
A. weigelti GMH Ce IV-3826	GT, MP 13	16.3 s	8.9 s	-	X-ray
A. weigelti? GMH Ce IV-2767a	GT, MP 13	16.6 d	8.6 d	8.0 d	isolated
A. weigelti? GMH Ce IV-2859	GT, MP 13	16.7 s	(8.8) s	-	isolated; medially broken
A. weigelti GMH Ce IV-4223	GT, MP 13	17.5 s	10.5 s	8.6 s	C: X-ray
A. weigelti GMH Ce II-4219	GT, MP 13	16.1 d	8.1 d	7.2 d	dorsally visible
A. weigelti GMH Ce IV-4332	GT, MP 13	17.0 s	10.1 s	-	X-ray CORR
Anthracobunodon? GMH Ce IV-2851a	GT, MP 13	15.3 s	(7.0) s	5.5 s	isolated; distally broken
Anthracobunodon? GMH XXXVI-320	GT, MP 13	15.5 s	8.4 s	6.5 s	isolated
Haplobunodon? GMH XLI-210	GT, MP 13	16.3 d	8.7 d	8.1 d	isolated
Masillabune franzeni GMH VII-58	GT, MP 13	(13) s	8.7 d	-	A: oblique position CORR
Cebochoeridae? GMH Ce III-4370	GT, MP 13	14.0 d	-	(5.2)d	isolated; proximally broken
Haplobunodontidae? GMH Ce IV-2767b	GT, MP 13	13.9 s	6.7 s	5.9 s	isolated
Haplobunodontidae? GMH Ce IV-2851b	GT, MP 13	(13) d	(7.9) d	6.2 d	isolated; proximally broken
Haplobunodontidae? GMH XXXVI-384	GT, MP 13	13.2 s	6.6 s	5.9 s	isolated
Dichobunidae? GMH Ce IV-2768b	GT, MP 13	9.8 d	5.2 d	4.3 d	isolated; juvenile
Dichobunidae? GMH XXXVI-360	GT, MP 13	12.2 d	6.3 d	5.3 d	isolated
Dichobunidae? GMH Leo I-2769	GT, MP 13	(12) d	6.6 d	5.8 d	isolated; proximally broken
Anthracobunodon neumarkensis GMH XVIII-787	GT, MP 12	16.4 s	8.5 s	7.3 s	isolated
Anthracobunodon? GMH XXII-790	GT, MP 12	15.8 s	7.8 s	6.8 s	isolated
Haplobunodon mülleri GMH XXII-553	GT, MP 12	14.7 d	7.8 d	7.3 d	isolated
Haplobunodontidae? GMH XXII-788	GT, MP 12	14.5 d	-	6.8 d	isolated; distally broken
Dichobunidae? GMH XXII-785	GT, MP 12	12.1 s	(5.8) s	4.9 s	isolated; distal end defect
Messelobunodon? GMH XIV-974	GT, MP 11	(15) s	(7) s	(5.8) s	isolated; distal end defect
Messelobunodon schaeferi SMF ME-501	Messel, MP 11	16.5	(9)	-	X-ray; B: estimated
Messelobunodon? schaeferi SMF ME-1001	Messel, MP 11	12.2	6.5	-	X-ray
Diacodexis cf. varleti GMH XIV-2616	GT, MP 11	11.2 d	6.0 d	5.2 d	isolated
Masillabune martini coll. POHL	Messel, MP 11	17.0	-	-	TOBIEN (1985: Tab. 6)
Messelobunodon russelli coll. LOUIS	Prémontré, MP 10	9.9	4.4	-	SUDRE & ERFURT (1996: 403)
Messelobunodon russelli coll. LOUIS	Prémontré, MP 10	9.6	4.8	-	SUDRE & ERFURT (1996: 403)
Messelobunodon russelli coll. LOUIS	Prémontré, MP 10	8.6	4.4	3.6	MARTINEZ & SUDRE (1995: Tab. 6)
Diacodexis gazini MNHN RI-426	Rians, MP 7	6.3	-	2.8	GODINOT (1981: 108f., Fig. 25)
Diacodexis metsiacus USGS 2352	Wyoming, Yale 55	10.2	5.2	-	measurement from cast

Anthracobunodon weigelti is characterised by a ratio of distal width to total length of about 1:1.8 (range 1.7-1.9). This is relatively broad in comparison to older species from MP 11 and MP 12 of the Geiseltal, and especially in comparison with the astragalus of *Diacodexis gazini* MNHN RI-426 from MP 7 with a ratio of 1:2.25. Proximally two sagittal orientated high crests are developed, which are higher than in *Messelobunodon* of Premontré and also in *Diacodexis* of Rians. The medial crest is lower than the lateral one, but more sharp-edged. The lateral crest ends anterior in the middle of the lateral side with a small prolongation carrying a planar, oval facet for the proc. coracoideus calcanei. In anterior view a line-shaped transversal tuberositas stretches between the plantar ends of both crests, see GMH Ce IV-2767a. There, *Haplobunodon mülleri* GMH XXII-553 displays a groove only. This tuberositas divides the two trochleas and gives the bone a waist-like taper. In dorsal view the lateral crest leads to a diagonal edge and joins with a prolongation of the medial crest; both enter a small ledge on the medial side. This ledge forms the dorsal border for the sustentacular facet in the form of a wall. Medially this articulation surface is marked by an oblique ridge and the plantar side by a furrow.

3.2.3 Navicular

Concerning the navicular of *Anthracobunodon weigelti* the specimen GMH Ce II-4226 gives the best information: For it, the bones were especially prepared and isolated from the articulated skeleton. In addition, the navicular of the undetermined haplobunodontid GMH XLI-210 was compared with other taxa.

In Ce II-4226 the width of the navicular is two thirds of the width of the caput tali. In dorsal view the bone has two longish concave articulation surfaces, corresponding to the form of the caput tali. These facets are separated by a small crest passing anteriorly in a short proc. extensorius. The process reaches into a fovea on the caput tali and marks the highest point on the navicular. In contrast, this articulation surface in *Messelobunodon* SMF ME-501 seems to be not so deeply hollowed out

Tab. 4: Navicular measurements of Geiseltal (GT) artiodactyls compared with European taxa [in mm].

A: largest length cranio-caudal on the dorsal side
B: largest width medio-lateral
C: largest height dorso-plantar on the anterior side
D: smallest height dorso-plantar in the middle of the medial side

species	locality	A	B	C	D	remarks
Anthracobunodon weigelti GMH Ce III-4221	GT, MP 13	7.0 d	-	5.5 d	3.5 d	A, C-D: CACM see Plate 1C
A. weigelti GMH Ce II-4219	GT, MP 13	7.3 s	(4) s	4.4 s	2.8 s	X-rays; B: estimated
A. weigelti GMH Ce II-4226	GT, MP 13	8.8 s	7.0 s	5.5 s	3.2 s	isolated, medially broken
A. weigelti GMH Ce IV-4332	GT, MP 13	9.5 s	(4) s	6.5 s	3.8 s	A-D: CORR see Plate 2B, B: estimated
A. weigelti GMH Ce IV-4334	GT, MP 13	8.5 s	-	6.7 s	3.8 s	medial side visible
Haplobunodon? GMH XLI 210	GT, MP 13	9.6 d	6.3 d	5.3 d	4.1 d	lateral side visible
Masillabune franzeni GMH VII-58	GT, MP 13	8.2 d	-	4.2 d	2.8 d	A, C-D: CACM
Haplobunodon mülleri GMH XXII-553	GT, MP 12	9.4 d	5.8 d	4.9 d	3.8 d	medial side visible
Messelobunodon? schaeferi SMF ME-1001	Messel, MP 10	8.1 s	-	6.5 s	4.2 s	medial side visible
Messelobunodon schaeferi SMF ME-501	Messel, MP 10	10.5 s	8.0 s	-	-	dorsally visible

On *Haplobunodon* GMH XXII-553 the anterior and medial side are rounded and rugged, and the posterior (caudal) wall is slightly concave and developed as tuberositas. In *Anthracobunodon* the outline should be the same, but the posterior wall is planar. In both genera the medial and anterior (cranial) wall are oblique to the dorsal side, giving the bone a wider dorsal than the plantar side. In contrast, the navicular of *Messelobunodon? schaeferi* SMF ME-1001 is pyramid-shaped laterally viewed and has a smaller dorsal side. Laterally GMH Ce II-4226 displays two separated articulation surfaces for the cuboid. The first one, dorsally situated on the anterior edge, is planar, longish oval and has a diameter of about 2.5mm. The second lies along the posterior wall and has a C-shaped outline, open to the middle. Both joints are completely divided by a groove. Interesting is the lack of the plantar orientated process in the CACM of *A. weigelti* Ce III-4221 and Ce IV-4334. In GMH XLI-210 this process is conspicuously latero-plantar orientated and sharply tapering, similar to *Messelobunodon* SMF ME-1001. The length is about 4.5mm long and an additional facet is visible near to the base of the process. This facet is concave, longish and has the dimensions of 2 x 4.2mm. It is regarded as joint for the entocuneiform. The navicular of GMH XXII-553, which is determined by the dentition as *Haplobunodon mülleri,* had such a process too. Therefore GMH XLI-210, represented by postcranial materials only, is regarded as *Haplobunodon?* The genus *Anthracobunodon* differs from dichobunids, and from some more primitive haplobunodontids in the reduction of this process as in *Caenotherium*.

Once, and only partly preserved in *Anthracobunodon*, is the plantar side of a navicular. In GMH Ce II-4226 are to be seen three facets, which are laterally situated. The biggest, anterior facet is convex and has a triangular outline with rounded edges. It serves for the ectocuneiform and is 4.1mm long and has a width of 3.3mm. On the posterior side the second (small oblique longish) facet stretches, which is a prolongation of the C-shaped posterior facet from the lateral side of the navicular. The third facet is a small convex swelling on the caudal side, well separated from the others. It is about 3mm long and 2mm width and similar to *Caenotherium* sp. NMB Sau.-1602a (HÜRZELER 1936: Taf. VIII,9). It is regarded as the articulation surface for the entocuneiform. Unfortunately, the complete shape is still unkown because of the broken medial part of this specimen. *Anthracobunodon* is different to *Haplobunodon*? GMH XLI-210, where the first and third facets are planar. The second does not exist. The first facet is also the biggest and occupies the anterior third of the bone (length x width: 4.2 x 3.5mm). Directly in contact in medio-caudal direction follows the third facet, smaller and oval with principal axes of 2.4 x 2.6mm. Laterally of it exists a furrow, separating the plantar process.

3.2.4 Cuboid

Details of the cuboid of *Anthracobunodon* are only to be seen in X-ray. In addition, other haplobunodontids and the small dichobunid Ce IV-2860 are compared.

All specimens with preserved cuboid and navicular have a length of the cuboid equal to the navicular (GMH: XLI-210, XXII-553, Ce IV-4332). The proximal side is divided into two articulation surfaces. The lateral surface is convex and serves as a joint for the calcaneum. This facet runs over the complete length of the cuboid and corresponds with the tip of the calcaneum. Therefore it is cranially dropping in length direction and oblique in medio-lateral direction, with its lowest point near the lateral side (see 0). The medial joint is sickle-shaped and continues the facet for the caput tali in accordance with the neighbouring navicular. The cuboid part of the articulation with the astragalus is significantly smaller than the navicular part. In *Haplobunodon mülleri* GMH XXII-553 with both preserved cuboid and navicular the relation is about 1:2.7.

In consideration of the details known from the navicular of *Anthracobunodon*, the completely medial visible side of the cuboid of *Haplobunodon*? GMH XLI-210 is used for comparison. There, the contact surface for the navicular is a rough area, which occupies two thirds of the cuboid and includes three articulation facets. The smallest facet lies caudally on the dorsal edge. It is planar, round and has a diameter of about 2.5mm.

Tab. 5: Cuboid measurements of Geiseltal (GT) artiodactyls compared with European taxa [in mm].

A: largest length cranio-caudal
B: largest width medio-lateral
C: largest height dorso-plantar including the plantar orientated process

species	locality	A	B	C	remarks
Anthracobunodon weigelti GMH Ce IV-4332	GT, MP 13	9.0 s	8.3 s	11.9 s	A, B: CORR see Plate 2B
A. weigelti GMH Ce II-4219	GT, MP 13	8.2 s	-	10.1 s	A, C-D: CACM
A. weigelti GMH Ce IV-4334	GT, MP 13	(9) s	-	10.6 s	lateral side visible
Haplobunodon? GMH XLI 210	GT, MP 13	9.6 d	7.5 d	11.3 d	medial and plantar side visible
Dichobunidae? GMH Ce IV-2860	GT, MP 13	8.1 s	6.2 s	9.3 s	full visible, isolated bone
Haplobunodon mülleri GMH XXII-553	GT, MP 12	(10) d	4.6 d	(9.2) d	latero-plantar side defect, with broken process
Messelobunodon? schaeferi SMF ME-1001	Messel, MP 10	8.2 s	5.3 s	8.5 s	medial side visible
Messelobunodon schaeferi SMF ME-501	Messel, MP 10	9.1 d	(7) d	14.6 d	lateral side visible; B: estimated

The second longish facet, which is slightly convex, is to be seen plantar from here on a probably specific caudo-plantar orientated process. In GMH XLI-210 this process comes out of the medial side and is strengthened in medial direction. The facet has the dimensions height x length of 4.8 x 2.4mm and ends before the process tapers. Because of the oblique part of the C-shaped facet of the navicular in GMH Ce II-4226 a corresponding process in the cuboid of *Anthracobunodon* should also have existed. This assumption is supported by the small cuboid of Ce IV-2860, which displays such a pronounced process carrying one continuous longish and slender facet. The articulation surface of *Anthracobunodon* seems to be directed more anteriorly as in GMH XLI-210. The third, anterior facet on the dorsal edge is poorly developed. It is suggested that it is more clearly visible in *Anthracobunodon*. Plantar of the navicular area exits a concave facet in GMH XLI-210, which is interpreted for the articulation with a relatively large ectocuneiform. In medially view the outline of this facet is rectangular with the dimensions length x height of 4.2 x 2.5mm. The facet ends caudally in the middle of the bone before the process starts.

The plantar side consists of an almost planar joint for the MT IV with a round outline and a diameter of 5.5mm followed caudally by a diagonal furrow. The caudal border of this side is built by the plantar process already mentioned. The development of this process is very different: Oblique tapering and finger-like in the dichobunid Ce IV-2860, stronger, wall-like and straight terminated in *Haplobunodon*? XLI-210. There, the process displays a longish articulation facet rising dorso-medially. Due to the furrow space results, used by the metatarsal processes at flexion. The lateral outside of the cuboid is similar to the navicular: rounded and porous.

3.2.5 Cuneiformes

Until now the morphology is problematic of the smaller distal tarsals in Eocene artiodactyls. Materials of these bones are very poorly preserved and mentioned in literature in passing only. Regarding the artiodactyls from Messel these bones are neither described in detail for *Messelobunodon* nor *Aumelasia*. TOBIEN (1985: 36) briefly mentioned the existence of an ectocuneiform in *Aumelasia martini*. HÜRZELER (1936: Plate VIII) shows a cube-like ectocuneiform and a relatively long entocuneiform for *Caenotherium* sp. NMB Sau.-1605a and NMB Sau.-1602a. He considered the mesocuneiform as an integrated part of the ectocuneiform, because he could not find an isolated example. There, the ectocuneiform has the same width as the navicular and a height of the half of the cuboid. In *Diplobune minor* UM ITM-43 SUDRE (1982) describes an entocuneiform, a small mesocuneiform and an ectocuneiform which is fused with MT I. For the North American *D. metsiacus* USGS 2352 from the Lysite, ROSE (1985:1216) mentioned that the ecto- and mesocuneiform are co-ossified dorsally and posterodorsally. The plantar and distal sides are still separated. In addition, there exists an entocuneiform. The only known Eocene artiodactyl with complete metatarsals and three independent cuneiformes are *Diacodexis pakistanensis* HGSP 300-5019 (THEWISSEN & HUSSAIN 1990: 45) from the lower Eocene of Asia and, according to GUTHRIE (1968), *Bunophorus* AMNH 14942. In recent artiodactyls pigs still have this primitive stage.

Unfortunately no artiodactyl cuneiformes are to be seen directly in the material of the Geiseltal collection. Neither of the X-ray investigations gave clear evidence. Probably Plate 1C/4 shows an ectocuneiform followed by the dislocated caput of metatarsus III. Anyway, the fact that the cuboid is higher than the navicular (see Ce IV-4332 in Table 5), gives an indication to the existence of this bone. An additional tarsal is needed to fill the gap between navicular and MT III . Further information is given by the facets on the plantar side of the navicular, described above. Accordingly, the form of the ectocuneiform should be cube-shaped with the dimensions length x width x height: 4 x 3.5 x 2mm. It is supposed that the ectocuneiform was similar to that of the lower Eocene *Bunophorus*, see GUTHRIE (1968: Fig. 3). There, the articulation surface to the navicular was slightly concave and planar to the MT III. The CACM of Ce III-4221 gives a similar impression. The contact to MT III could be slightly concave. Unfortunately, it cannot be excluded that the CACM is interfered with by fragments of the distal calcaneum.

No clear indication exists concerning the mesocuneiform in *Anthracobunodon*. No radiography displays this tarsal. It is supposed that the mesocuneiform was already fused with the ectocuneiform. As mentioned above the incorporation of this bone starts in the lower Eocene and is finished in the upper Eocene, see *Preatragulus* (VISLOBOKOVA 1998: 14). The similarity of other tarsal characters with *Caenotherium* sp. makes the preservation of a primitive status, as in *Diplobune minor* ITD 43 (SUDRE 1982: Plate 2) or *Sus*, unlikely. However, the existence of three independent bones cannot to confirmed.

The third facet on the plantar side of the navicular in GMH XLI-210 and Ce II-4226 vouches for an independent entocuneiform. If this bone articulates directly with the navicular and metatarsal II, as in *Caenotherium* sp., NMB Sau.-1605a the shape should be longish with a concave dorsal facet. On the plantar side should be a facet for MT II. This assumption is supported by CACM of Ce III-4221 and the CORR of Ce IV-4332, see Plate 1C/14 and Plate 2A/7. In both X-rays are displayed oval bones which fit these criteria. The length and height are 4.5 x 5.8mm for *A. weigelti* Ce III-4221 and 3.8 x 4.2mm for Ce IV-4332. The outline of these bones is similar to *Caenotherium*. In *Anthracobunodon* the dorsal facet is slightly concave. The plantar side is rounded, without a special formed facet for a metatarsus II. An articulation between entocuneiform and a residual MT I, as considered in *Diacodexis* by ROSE (1985:1216), is to be excluded, because of the lack of a MT I. The small bone fragment in Plate 1C/6 belongs to the proximal part of MT II. From lateral to medial side the relations of the lengths between the fifth and the other metatarsals are about 1:1.27:1.28 : 1.

4 Reconstruction and Comparisons

On the basis of isolated material, CACM- and CORR-images were produced manually for schematic reconstructions of the basipodium. The composition of the tarsus is proximally: Os tarsi tibiale (astragalus) and os tarsi fibulare (calcaneum). Distally one can identify: Os tarsi quartum (cuboid) and probably three cuneiformes. Intercalated between these rows is the os tarsi centrale (navicular), see Fig. 1.

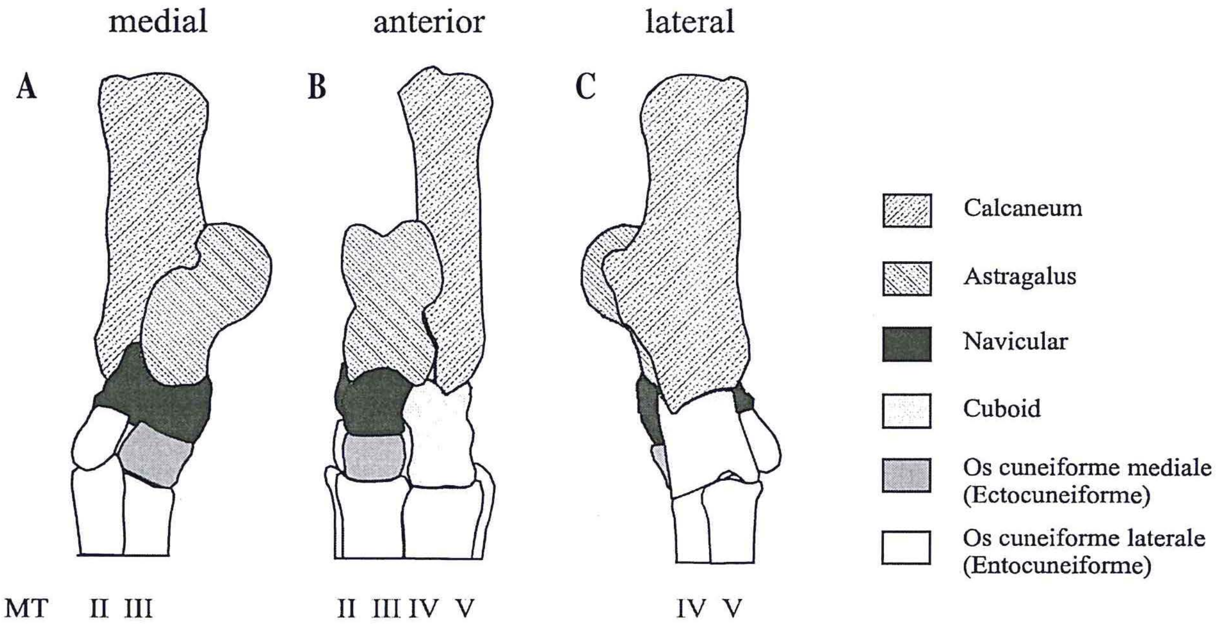

Fig. 1: Graphical reconstruction of the left tarsus of *Anthracobunodon weigelti* HELLER, 1934 from the middle Eocene Geiseltal (MP13).

Clearly visible is the separation of navicular and cuboid, see Plate 2B. This primitive character is shared with lower Eocene diacodexeids and dichobunids from Europe (SCHLOSSER 1887; FRANZEN 1981, 1983, 1988), North America (ROSE 1982, 1985, 1988) and Asia (THEWISSEN & HUSSAIN 1990) as Oligocene nonruminants like *Caenotherium* (SCHLOSSER 1887: Plate 1/20-25) as well. During the upper Eocene ruminants already occur in Asia (VISLOBOKOVA 1998), which display more progressive traits, as for example an elongation of the distal limb segments and fusions in the basipodium. Therefore it should be possible to trace back general tendencies of the tarsus reorganisation into the middle or lower Eocene.

The reduction of the fibula is one of these tendencies common in all artiodactyl groups. For the haplobunodontid *Anthracobunodon weigelti* there still exists a complete fibula, but the diaphyse is very thin, see Plate 2A/2. In correlation the size of the fibular facet on the calcaneum becomes smaller, which is visible at *A. weigelti* (MP 13) compared with *A. neumarkensis* (MP 12) from the Geiseltal. In basic features the calcaneum of *Anthracobunodon* is similar to other Eocene and Oligocene artiodactyls (see 3.2.1). The differences are only gradual: The mentioned size of the fibular facet, the size of the sustentaculum tali, the height of the proc. coracoideus, the depth of the lateral groove and the length of the tuber.

The last mentioned differences suggest the existence of special functional adaptations in Geiseltalian artiodactyl taxa. For example Table 2 displays variable proportions of the length of the tuber to the total length of the bone between 1:1.7 (*Meniscodon picteti*) to 1:2.0 (*Anthracobunodon weigelti*) and 1:2.3 (*Anthracobunodon neumarkensis*). Lower Eocene species already have a relatively long tuber, see the proportion 1:1.9 of *Diacodexis metsiacus* USGS 2352. Therefore ROSE (1982: 623) regarded *Diacodexis* as already highly cursorial adapted and not as a stem artiodactyl. Relatively short calcanei are known from middle Eocene artiodactyls. Therefore it is questionable whether the prolongation of the tuber is an advanced state or the reduction in some groups. The development of the non-cursorial and relatively heavy morphotype in the non-neoselenodonts could be secondary as the modern cursorial, gracile type as well. A Paleocene or lower Eocene non-gracile ancestor is still unknown. Generally it is regarded that the primary morphotype was a generalized, non-cursorial adapted animal. The elongation of limb elements should be an advanced stage. In *Anthracobunodon* the tarsus becomes more robust, the calcaneum shorter, see the proportion between *A. weigelti* and *A. neumarkensis* in Table 2. Either the genus indicates a reversal in this development within the middle Eocene haplobunodontids or the genus indicates the prolongation of a primitive group, which has a "suiform" morphology with bunodont dentition. The first possibility seems to be more likely because of the lack of generalised bunodont forms in the lower Eocene.

Compared with the older *Diacodexis* from Premontré or *Messelobunodon* from Messel the astragalus of *Anthracobunodon* displays the following tendencies: The deepening of the trochlea tali; caput tali and trochlea tali come in a vertical position above each other; the broadening of the caput tali and the elongation of the sustentaculum tali. Again, these changes are gradual, see the relation between the total length (A) and the width of the caput tali (B) in Table 3. For example, the caput of the astragali from locality XXII are slender and shorter than those from locality Ce IV. The size of the distal articulation facets for the cuboid and navicular is variable, which are differentiated by a small crista. The big astragali in Table 3 from MP 12, which probably all belong to *Anthracobunodon neumarkensis*, have two nearly equal facets. All younger Geiseltal artiodactyls from MP 13, including *A. weigelti,* have a dominating navicular facet. The strengthening of the navicular facet is already to be seen in older artiodactyls (MP 11) of the Geiseltal. The very small astragalus of the diacodexeid GMH XIV-2616 displays a reduced cuboid facet of only 30% of the distal width. The dorsal-plantar extension of the sustentacular facet is about 50% of the total length in *Anthracobunodon*, which is relatively short in comparison to younger artiodactyls but more or less equal to *Messelobunodon* from Messel. It suggests that the variety and functional adaptations of astragali mentioned from MARTINEZ & SUDRE (1995) for M18 to M28 go back into the middle Eocene. For this time the extension of the articulation facets and several indices are regarded as characteristics for species too.

The cuboid displays two tendencies: The stabilisation of the articulation with the calcaneum (see 0); and the stabilisation of the articulation with the metapodium. The last mentioned process is realised by an enlargement of the facet for the metatarsus IV. The surface of this joint becomes planar. In contrast, the facet for the metatarsus is still concave in *Messelobunodon* from MP 11 and indicates more mobility. The concentration of the movement in the proximal tarsal row is regarded as an advanced cursorial adaptation, which is probably typical for all artiodactyls.

The strengthening of the navicular gives the second part of the fortification between the proximal and distal tarsal row. Paraxonically one part of the body mass is diverted via this bone and the ectocuneiform to metatarsus III. In accordance with the broadening of the caput tali the navicular becomes wider and higher, see for example the relation between the height (C) on the anterior side and the height (D) on the medial side in Table 4. As a consequence, the connection to the ectocuneiform become more stable by planar facets. Neither the CACM of Ce III-4221 nor Ce IV-4334 (see Plate 2b), show a plantar orientated process on the navicular. This process is still relatively long in the lower Eocene *Bunophorus* (GUTHRIE 1968: Fig. 3c,d) and *Messelobunodon*? SMF ME 1001 from MP 11. If this lack is not artificial, it could indicate the beginning of the reduction of the entocuneiform because this bone stands in articulation with the process.

Due to the lack of isolated carpals in the Geiseltal collection the reconstruction of the carpus is mainly based on two specimens: *Anthracobunodon weigelti* GMH Ce III-4221 and Ce II-4226. Additionally *Haplobunodon mülleri* GMH XXII-553 was used for comparison. The two-dimensional graphical reconstruction in Fig. 2 results from the evaluation of CACM pictures (see Plate 1 b-c) and about 100 CT sections.

The carpus consists of two rows, proximally from the medial to lateral side: Os carpi radiale (scaphoideum), os carpi intermedium (lunatum), os carpi ulnare (triquetrum) and the os carpi accessorium (pisidium). Distinguishable in the distal row are: Os carpi primum (trapezium), os carpi secundum (trapezoideum), os carpi tertium (capitatum) and os carpi quartum (hamatum). An additional fifth element, called lateral unciform by THEWISSEN & HUSSAIN (1990) as mentioned in the most primitive artiodactyl *Diacodexis pakistanensis,* could not be found. In general, the carpus of *Anthracobunodon* displays a composition common to North American diacodexeids of the lower Eocene. Specialised features, such as reductions of distal carpals, known from the upper Eocene *Praetragulus* (VISLOBOKOVA 1998: Fig.7), are not to be seen. Anyway, gradual differences are to be noticed in the size and position of the carpals.

As in the tarsus, the main articulation takes place between the proximal row and the zeugopodium. Relatively deep concave joints indicate a higher degree of freedom between basipodium and metapodium, as for example in some Oligocene artiodactyls indicated in Fig. 2E-G. Due to the plane articulation surfaces the degree of freedom is small within the basipodium and between the distal row and the metacarpals. Similar to the strengthening of calcaneum and astragalus (respectively cuboid and navicular) the radiale, intermedium and quartum and tertium strengthen as well.

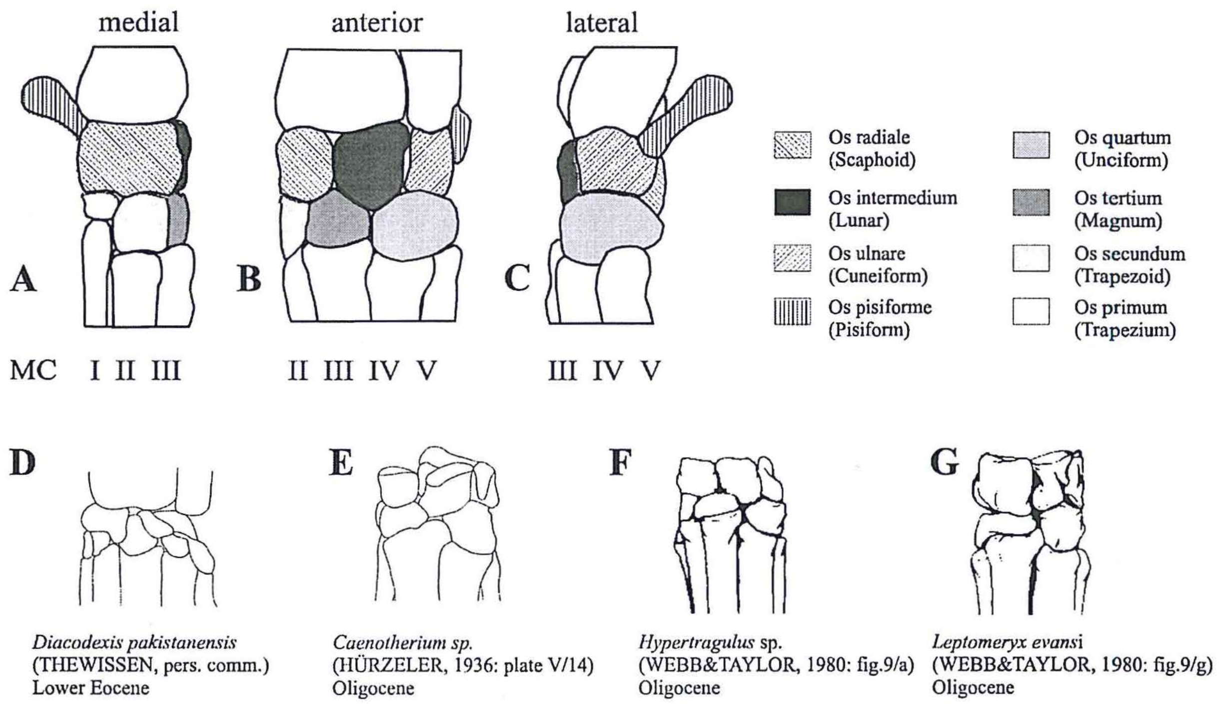

Fig. 2: Graphical reconstruction of the right carpus of *Anthracobunodon weigelti* HELLER, 1934 from the middle Eocene Geiseltal (MP13) compared with other Paleogene artiodactyls (D-G).

The intermedium is bigger and has a more central position compared with *Diacodexis*. This bone transmits the body weight to the os tertium and os quartum, which is very compact. The increasing of the intermedium seems to be a general tendency in all artiodactyls. The acute form on the palmar side gives an overlay with the distal row similar to brickwork.

Proximally the radiale seems to have still a relatively small articulation surface with the radius. This is similar to *Hypertragulus*, but not *Leptomeryx* (WEBB & TAYLOR 1980, SUDRE 1995) or recent ruminants. There, the radiale reaches until the middle of the carpus anteriorly viewed. Distally the radiale is still in contact with the secundum and tertium. In higher ruminants the distal row consists of the tertium and quartum only.

The ulnare is relatively large in correlation to the size of the distal end of the ulna. In younger ruminants the articulation of the distal zeugopodium is mainly given by the radius, or the ulna is more or less incorporated in the radius (tylopods). *Anthracobunodon* resembles in the proportion of the width radiale : intermedium : ulnare of about 1.6 : 2 : 1 more the recent *Sus*. An additional similarity is the slits between the proximal carpals, especially between intermedium and ulnare. Fig. 2B indicates a longish oval gap near the quartum, which is to be found in a round shape in *Sus* too. Close contacts between the carpals are to be seen only in vertical direction in correlation with the vertical transmission of the body weight.

The quartum appears in the CT sections as the carpal with the largest articulation surface. Together with the radiale and ulnare it displays the thickest compacta, giving these bones a high internal stability. The size of the neighbouring tertium is relatively small compared with *Praetragulus* and *Caenotherium* but similar to the reconstruction of *Plesiomeryx* by (SCHLOSSER 1887: Plate 1/5). The enlargement of these two bones is a general tendency in artiodactyls in connection with the paraxonic strengthening of MC III and MC IV. The size difference between quartum and tertium in a middle Eocene artiodactyl indicates an independent enlargement of the quartum at least during the lower Eocene or - more likely - earlier. One reason for the magnification of a bone could be the incorporation of other skeletal elements. The description of an additional "lateral unciform" in the lower Eocene *Diacodexis pakistanensis* by THEWISSEN (1990) could explain the large size of the quartum by an unification of another lateral carpal of the distal row. It is supposed that the fifth os carpi distale laterale, known from primitive tetrapods, is already reduced in basic mammals (STARCK 1987: Abb. 503). If the existence of such an additional distal carpal can be proved in more artiodactyls than the root of the order could be focused in more detail. Unfortunately, the anatomy of the hand is relatively unknown in arctocyonids, the presumed precursors of artiodactyls by ROSE (1996). The mentioned similarities in dental and postcranial traits indicate that the separation of artiodactyls was at least in the Palaeocene. In the lower Eocene the paraxonic structure was already realised in the hindlimb and in the middle Eocene in the forelimb.

The applied X-ray methods open a new access to morphological information in the Geiseltal material. They are especially useful for the investigation of the rear side of smaller specimens, which are embedded in paraffin. Only by this technique was it possible to describe new details in the basipodium of *Anthracobunodon* including micro-structures. The morphology of the basipodium indicates evolutionary trends correlated to the locomotion of this haplobunodontid. In artiodactyls and other "ungulates" these specialisations are fundamental for the understanding of phylogenetic relationships. Due to the relatively good fossil preservation and the known lithostratigraphical position of the localities (see FRANZEN & HAUBOLD 1987) reinvestigations of other groups with similar methods offer the opportunity to enlarge significantly the data base for morphological comparisons and interpretations of the phylogeny and palaeoecology in the middle Eocene faunas.

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Anschrift der Autoren:

Dr. Jörg Erfurt
Martin-Luther-Universität Halle-Wittenberg
Institut für Geologische Wissenschaften und Geiseltalmuseum
Domstraße 5
D-06108 Halle (Saale)

Dr. Jörg Habersetzer
Forschungsinstitut Senckenberg
Senckenberganlage 25
D-60325 Frankfurt/M.

Plate 1

Anthracobunodon weigelti HELLER, 1934 GMH Ce III-4221.

A: Situation in situ during the excavation campaign in 1932 in the Geiseltal lignite pit. The arrow indicates the scan direction from cranial to caudal.
Picture: Archive Geiseltalmuseum, Martin Luther University Halle.

1 Scanning area of the left carpals and metacarpals
2 Scanning area of the right carpals and metacarpals
3 Scanning area of the right tarsals and metatarsals

B: Computer Aided Contact Microradiography of both forelimbs. Right: Left forelimb in medial view. Left: Right forelimb in lateral view.
Picture: J. HABERSETZER, Research Institute Senckenberg Frankfurt.

1 Ulna d
2 Radius d
3 Os carpi intermedium d
4 Os carpi radiale (Scaphoideum) d
5 Os carpi ulnare (Cuneiform) d
6 Metacarpus III d, partly visible and underneath MC IV
7 Metacarpus IV d,
8 Metacarpus V d
9 Metacarpus II d, distal end partly visible underneath MC IV
10 Phalange II/2 d in articulation with Phalange II/1 d
11 Phalange V/2 d in articulation with Phalange V/1 d
12 Phalange I/2 d in articulation with Phalange I/1 d
13 Ossa sesamoidea phalangis primae probably belonging to Metacarpus V d
14 Metacarpus I d
15 Os carpi quartum (Unciform) d underneath caput of metacarpus V d
16 Os accessorium d
17 Phalange III/3 d in articulation with Phalange III/2 and Phalange III/1 s
18 Phalange II/3 d in articulation with Phalange II/2 and Phalange II/1 s
19 Ossa sesamoidea phalangis primae of Metacarpus III s
20 Ossa sesamoidea phalangis primae of Metacarpus I s
21 Os carpi secundum (Trapezoid) s
22 Os carpi primum (Trapezium) s
23 Os carpi radiale (Scaphoideum) s
24 Os carpi tertium (Magnum) s
25 Os carpi intermedium (Lunar) s

C: Computer Aided Contact Microradiography of right hindlimb, lateral view.
Picture: J. HABERSETZER, Research Institute Senckenberg Frankfurt.

1 Tuber calcanei d
2 Tibia d
3 Astragalus d
4 Cuboid d, plantar part
5 Navicular d
6 Metatarsus II d proximally broken
7 Metatarsus III d proximally broken
8 Phalange II/1 d in articulation with Phalange II/2 and II/3 s
9 Phalange III/2 d in articulation with the destroyed Phalange III/3 s
10 Phalange IV/1 d, compressed
11 Metatarsus IV d
12 Lateral Metatarsus (MT V d?) dislocated underneath MT III and MT IV d
13 Metatarsus IV d, caudal orientated process
14 Os cuneiforme laterale (Entocuneiform) d
15 Cuboid d, proximal part
16 Caudal vertebrae

Plate 1

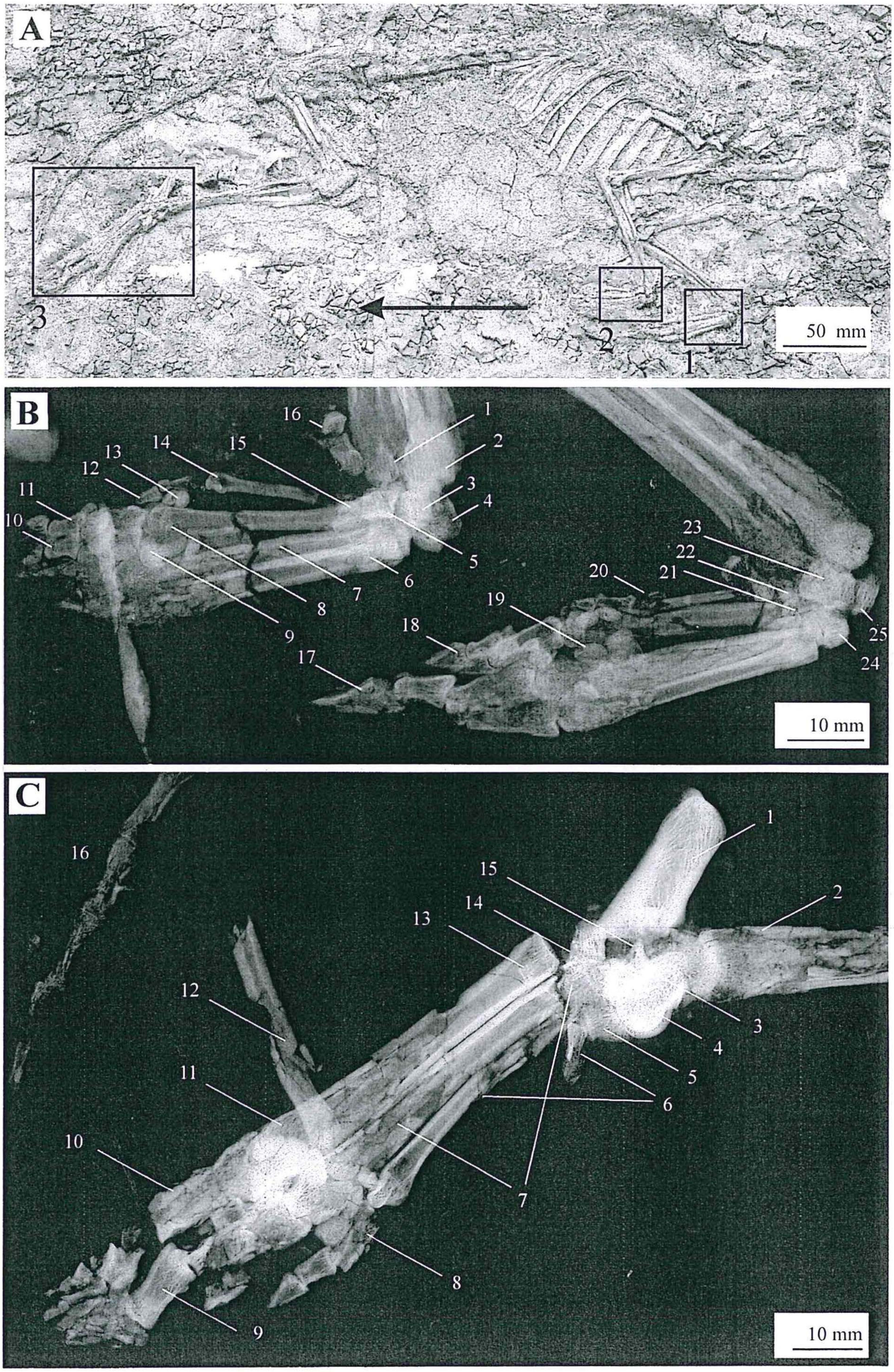
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Plate 2

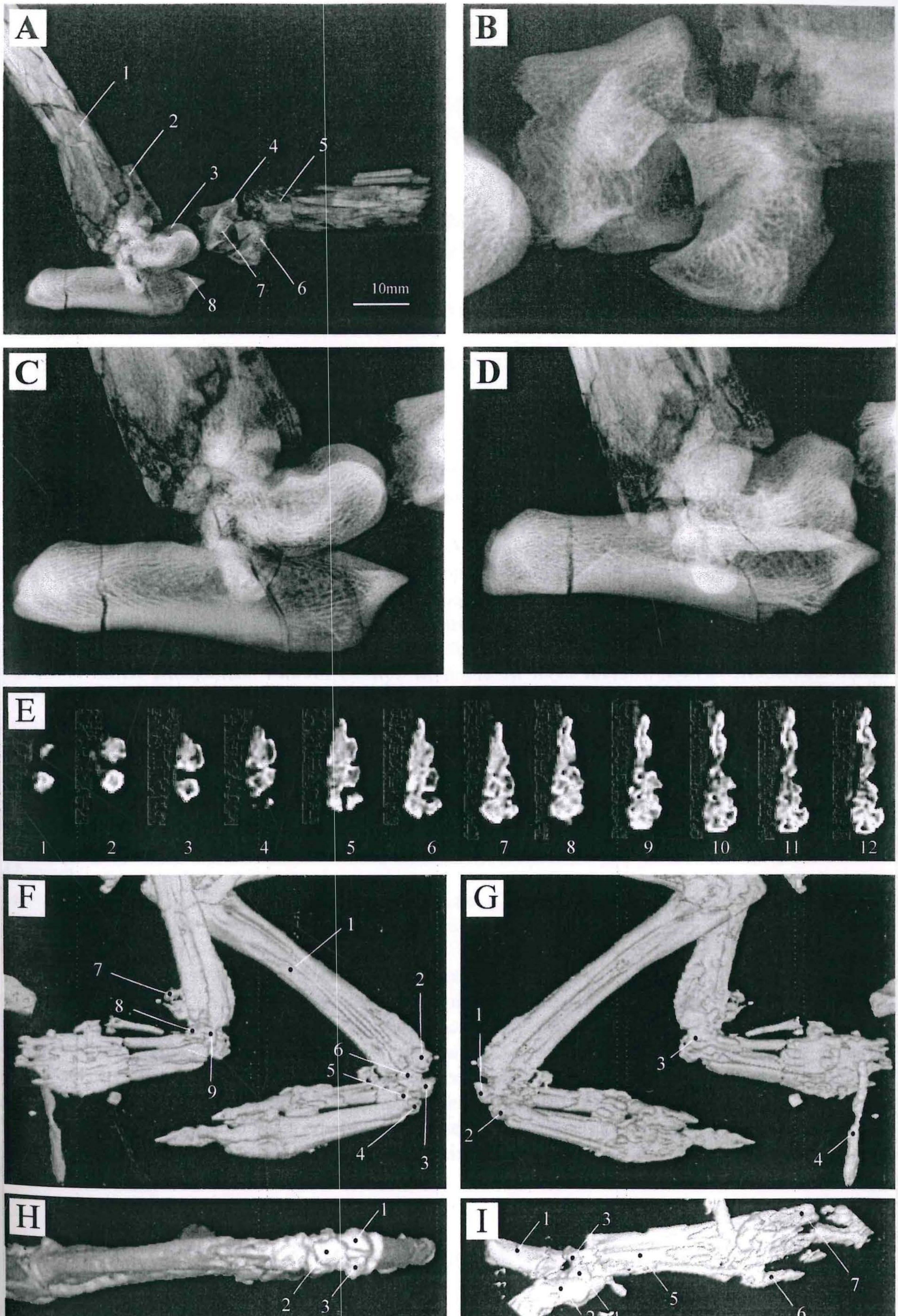
Anthracobunodon weigelti HELLER, 1934 GMH Ce IV-4332.

A: Continuous Online Recalibrated Radiography of the right hindlimb. Medial view from the rear side with the complete tarsus, parts of tibia, fibula and metatarsals.
 1 Tibia s, distal part
 2 Fibula s, distal part
 3 Astragalus s
 4 Cuboid s
 5 Metatarsals s, compressed proximal parts
 6 Navicular s
 7 Entocuneiform s, underneath the cuboid
 8 Calcaneum s
B: Continuous Online Recalibrated Radiography of the cuboid and navicular. Medial view from the rear side, magnified and 15° vertically rotated.
C: Continuous Online Recalibrated Radiography of the calcaneum and astragalus. Medial view from the rear side, magnified and 15° vertically rotated.
D: Continuous Online Recalibrated Radiography of the calcaneum and astragalus. Medial view from the rear side, magnified and 30° rotated.
Pictures: J. HABERSETZER, Research Institute Senckenberg Frankfurt.

Anthracobunodon weigelti Heller 1934, GMH Ce III-4221.

E: Computer - Tomography of the left forelimb, see Plate 1A/1. From left to right: Sequence of 12 scanned slices in cranial to caudal direction. First slice displays a cross-section of the intermedium, last slice with cross-sections of the proximal metacarpals below.
F: Three dimensional reconstruction of the CT-data. View from the original side of the specimen to both forelimbs.
 1 Ulna s
 2 Radius s
 3 Os carpi intermedium s, medial side
 4 Os carpi tertium s
 5 Os carpi secundum s
 6 Os carpi radiale (Scaphoid) s
 7 Os accessorium d
 8 Os carpi ulnare d
 9 Os carpi intermedium d, lateral side
G: Three dimensional reconstruction of the CT-data. View from the rear side of the specimen through the matrix to both forelimbs.
 1 Os carpi intermedium s, lateral side
 2 Os carpi quartum s, lateral side s
 3 Os carpi radiale d, lateral side
 4 Calcification of fissure in the matrix
H: Three dimensional reconstruction of the CT-data. View from the anterior side of the specimen through the matrix to the left forelimb.
 1 Os carpi quartum s
 2 Os carpi intermedium s
 3 Os carpi tertium s
I: Three dimensional reconstruction of the CT-data. View from the plantar side of the specimen through the matrix to the left hindlimb.
 1 Tuber calcanei s
 2 Astragalus s
 3 Cuboid s
 4 Navicular s
 5 Metatarsus III s, posterior side
 6 Phalange II/2 s in articulation with Phalange II/3 s, posterior side
 7 Phalange IV/1 s
Pictures: R. BECK, Röntgenklinik of Martin - Luther - University Halle.

Plate 2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